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THE GLACIAL BORDER — CLIMATIC, SOIL, AND BIOTIC FEATURES

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VEGETATION AND CRYOPLANATION

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The general subject of this symposium is the behavior of plants, animals, and biotic communities with relation to the southern boundary of the glacial tills and other deposits that date from the Pleistocene ice advances. There is in this subject the assumption, or at least the working hypothesis, that the glacial boundary *has* significance to the present distribution and behavior of the living inhabitants.

There is no question that the boundary is a demonstrable fact, and that it is marked by differences in soils and land forms. Furthermore, it has a historical significance. There is in our subject the further hypothesis that the behavior of the biota and biotic communities on either side of the boundary is related in some way to historical facts rather than to present ones alone. There is a suggestion that the occurrence and local distribution of the biota cannot be understood simply by analysis of climatic, edaphic, and biotic factors of the environment on either side of the boundary at a point in time, but that they must be interpreted also in the light of the history and inheritance of the organisms themselves in relation to the history of the soils and land surfaces. In brief, it is suggested that to reach a reasonable understanding of the present behavior of the biota we should endeavor to reconstruct the landscapes in the region of the glacial boundary as they have developed in postglacial time.

In whatever way we choose to interpret the biota and its geography, we must begin with "site" or "fundament." There must be a "place" into which the biological elements of the landscape can come. American plant geographers, with their predilection for the "dynamics" of vegetation, have always been greatly concerned with land surfaces and soils. They have been particularly concerned with the mutability of the terrain because of their emphasis upon the study of vegetational change. We have experimented with interpretations of climatic change in a few places, particularly in the West, but we have built our ideas of vegetational development very largely upon physiographic change.

Out of this has come what we commonly call "physiographic ecology." Although some of its roots are to be found in a few isolated ideas derived from the Old World, physiographic ecology is based principally upon an American idea, developed in the temperate parts of the upper Mississippi basin and the Great Lakes region. It had its beginnings about 50 years ago when the terms "peneplain," "monadnock," and "cycle of erosion" became current in physiographic study. This was the period in which modern physiography was growing in America under the influence of W. M. Davis (1909) and his co-workers. There appeared the idea of a cycle of erosion wherein mature topography, uplifted by diastrophism, was rendered youthful again through renewed erosion, by running water, of the old surfaces. Upland water tables would then be lowered, and materials derived from the uplands would be transported and deposited again on flood plains, upon which would be re-established a degree of physical stability. There were, of course, many variations of this theme of the mutability of the terrain, but the principal agents of change were usually running water or wind.

In such an ideological setting there was fertile ground for the development of ideas of change in the botanical landscape. We had a series of research projects whose results have become classic in American plant ecology. Cowles (1901) produced his masterly analysis of the vegetation of the Chicago region, and cleverly related vegetational development to the evolution of land forms. He made an equally searching study of the great sand dune areas at the south end of Lake Michigan (Cowles, 1899). Transeau (1903, 1905–06) took up the study of the development of vegetation on poorly drained land, and presented papers on the bog plant societies of North America. Jennings (1909) caught the idea of relating vegetational development to certain shore forms on the Great Lakes. All of these papers appeared within a period of ten years, between 1899 and 1909. The ideas were carried further, with considerable broadening, by Miss Braun (1916) in her physiographic ecology of the Cincinnati region, and by Nichols (1913–20) with his vegetation of Connecticut.

In more recent years the idea has been given still wider application by Fernald (1931) in his detailed studies of species distribution and specific differentiation in eastern North America, and by Miss Braun (1940) with her description and analysis of the undifferentiated deciduous forest communities of the ancient Appalachian Plateaux. Here the idea has been carried beyond local application restricted to relatively small areas, and has been applied on a geologic time scale, involving changes of land surfaces and vegetations dating into the Tertiary. Clements (1916) went still further and conceived of gigantic succession complexes that might be related to the great geologic eras of the earth.

This idea, with all its ramifications, has become a part of the very fabric of our thinking in plant geography. Almost without our knowing it, the idea has greatly influenced some of our most basic concepts, such as that of the plant association and the nature of succession.

The idea was worked out in the temperate parts of North America, a fact which is commonly lost sight of in our preoccupation with the complex problems to which it has given rise. One of the primary characteristics of the development of land forms in this region is the existence of periods of relative physical stability in the soils. Considerable periods of time are required to erode an uplifted surface and to deposit its materials elsewhere. During these processes there are times of stability which are long enough to embrace many generations of our longest lived plants. This applies in varying degrees to the time it takes to fill a pond with vegetation, or to reactivate a sand dune, or to move a sand spit along the shore of a lake.

In these times of physical stability in the soils, complex communities of plants and animals have time to form, and what we call "dominance" almost invariably appears in them. The vegetation has time to react upon the raw fundament, and plant communities by their life and development alter the sites upon which they occur. The phenomenon of succession appears, and many students have gone so far as to use a "biological" definition of succession, wherein it is conceived that the only true succession is one that is brought about by the reaction of plants and plant communities upon the site and upon each other (Phillips, 1935).

Some of us have tried to work out plant successions outside of the temperate zone. To put the matter mildly, we have had difficulties in applying the ideas derived from our training and experience in the temperate regions. We have found that the farther we go, phytogeographically, toward the Arctic or the Tropics the greater the difficulties become. It is only natural that we should carry our methodologies and assumptions with us as we go, and it is also natural that we should be loath to discard or seriously modify them when we find them inadequate.

One of the first questions that arises is in the application of the idea of dominance to complex communities. In the arctic and alpine tundra we have communities of relatively few species, but when one tries to describe them in terms of dominance or primary species he finds himself merely listing a considerable part of the flora. Antevs (1932) had this difficulty when he was describing the alpine communities in the White Mountains of New England, and Polunin (1934–35) found it extremely difficult to do at Akpatok Island. Polunin's (1948) recent study of plant communities in the Eastern Arctic resolves itself into a compendium of variable species complexes that reappear with endless variety in one locality after another. It was this that Griggs (1934) was talking about when he said that the tundra flora of Alaska acted like a ruderal or weedy flora with no apparent rhyme or reason in its local assemblages. In all of these cases, we see a prime characteristic of temperate vegetation non-existent or very poorly developed in the Arctic.

Another of the attributes of plant communities, successional development, also becomes extremely difficult to document and prove as we go away from the temperate zone. Vegetational change does occur naturally, but to establish it within a "biological" definition, or in terms of any physiographic progression with which we are familiar, commonly becomes impossible.

In the boreal regions of America, we deal with topography which in many cases is extremely youthful. Water tables and lake shores fluctuate much more than they do in the temperate zone. One wonders what would happen to our ideas of the development of vegetation on the shores of Lake Erie if the water level of this lake should rise 8 or 10 feet every 50 years or so and then return to its former level; but that is what happens at Lake Athabaska. Whole lake basins composed of myriads of small bodies of water interspersed with swamps and bogs are having their ground water levels reduced by the erosion of friable barriers such as glacial moraines. Other lakes are being formed as "thaw lakes" in areas underlain by perennially frozen ground (Hopkins, 1949). Such bodies of water appear, develop marginal vegetation and then disappear when the vagaries of seasonal thaws open underground drainage channels. Ice-push is enormously effective in modifying shore forms, and is a factor which is insignificant in most of the temperate zone. The result is that vegetation around lakes and ponds in the far north commonly gives but little indication of regular successional stages in the development of organic deposits.

Perhaps the most nearly authentic natural successions in the North, with the exception of a few secondary ones, are on river islands and flood plains. Here again, however, excessive flooding due to damming by ice and driftwood is so common that it becomes difficult to infer natural biological successions.

Evidences of succession in the Arctic, when they are carefully examined, commonly prove to be so fragmentary and so isolated in the total context of the vegetation that they cannot be strung together into recognizable trends toward equilibrium. Approaches to equilibrium or relative stability, such as we find in temperate regions and are wont to call "climaxes," are almost impossible to define in the Arctic and much of the Subarctic. At best they are ephemeral in time and space.

With the ideas of dominance and succession so difficult to apply in the North, it behooves us to re-examine some of our basic premises with regard to the relations between the development of vegetation and the development of land forms. Dominance and succession are both basic attributes of vegetation in the temperate regions, and I have suggested above that they both arise from a degree of physical stability which in turn is a fundamental attribute of the land surfaces. We are entitled to ask whether there can be something wrong with the physiographic premises upon which we are basing our work in the boreal regions.

The student of land forms brought up in temperate America, when he goes into the boreal regions, sees a great variety of forms with which he is totally unfamiliar. He is apt to be as bewildered as a northern botanist who makes his

FIGURE 1. Stone polygons on a limestone mountain in northeastern British Columbia. The fine-textured materials in the centers of the polygons are so actively "churned" by frost action that only a few hardy plants can withstand the frequent physical disturbance of the soil.

first excursion into the tropics. Our physiographer has learned that it is possible for rocks to be cracked by frost. But he has never seen such active frost riving as he sees in the Arctic and Subarctic. Large boulders are commonly broken into little pieces by frost, with all the fragments lying about in the vicinity. He will see massive angular boulders lying about a central core. With heavy machinery he could put them back together to form a rock as big as a house, and he is forced to the conclusion that the frost riving he sees now is child's play to what must have occurred in the past.

He comes upon great fields of rock, called "block fields," that are composed of large boulders, many of them angular, and obviously formed by the break-up of still larger ones. No physiographic process that he has ever heard of in the temperate zone is adequate to explain them.

The land surface is marked by a multitude of terrace forms. Some of these are several feet high and many feet long. Others are tiny affairs, only a few inches high and wide. If he has the time to dig trenches through such terraces, he finds that many of them are still active in formation and movement.

On more or less level surfaces he is confronted with curious polygonal arrangements of materials. The polygons may be composed of fine or coarse material,

FIGURE 2. Large "fossil" stone rings in southwestern Yukon, 6–10 feet in diameter.

FIGURE 3. Cryoplanation terraces on a tundra-covered mountain slope in southwestern Yukon.

and they may vary in size from the width of his hand to many feet. On slopes he finds long stripes of loose stone trending at right angles to the contours, and on very gentle slopes he finds these stripes merging into a series of combinations with the polygonal arrangement. A surprising proportion of the stones will be found to be standing on edge. On high mountain slopes, he will see remnants of bed rock standing up above the general level like monuments. These remnants are exfoliating actively, breaking up under the influence of frost. They have a configuration in profile which is utterly strange to him, because, although they are rapidly disintegrating, there is no talus accumulation at their bases. In fact, they are apt to show some overhang at the base. The surfaces of the gentle slopes below these monuments are strewn with rock fragments that have fallen from them, and it is obvious that the fragments are moving away down slope from the base faster than they can accumulate.

He will be impressed by the relative insignificance of stream cutting and deposit. Flood plains are small in breadth and depth. There is very little evidence of these processes except where great glacial streams issue from the mountains. Another striking feature of the landscape is the broad rounding of slopes. The general contours of these slopes are not those that we have learned to associate with down cutting by streams.

From all of these observations, our student of land forms gets the impression that the surface materials of the land are in motion, slow motion though it may be. He must also conclude that this motion has been more active at some time in the past than it is now. He soon begins to associate most of these features with the action of frost upon the soils.

Each year in the boreal regions the ground freezes to great depths. In many parts of the Arctic and Subarctic there is perennially frozen ground beneath the surface. In fact, it is now computed that about one-fifth of the earth's surface is underlain by perennially frozen ground (Jenness, 1949). During the spring of each year the surface materials thaw out. But there is a relatively long period during which the temperature fluctuates diurnally around the freezing point. Each time the water in the soil freezes it expands; and the effective expansion is in a direction at right angles to the freezing surface. When the soil thaws again its particles fall vertically, so that if the surface has any slope, they tend to move down grade. It is obvious that if freezing and thawing are to be effective, there must be a supply of water. One of the characteristics of freezing soil is that it can absorb and hold much more water than unfrozen soil. It has a tendency to absorb water as it freezes (Taber, 1943). Consequently many frozen soils are water-logged so that when they thaw they are almost fluid and have a tendency to flow down slope en masse. This greatly enhances the rate of movement of materials.

From the standpoint of vegetation, one of the principal results of this process is instability. The soils, even under forest or heavy turf, will move, often in masses. The result is the physical dislodgment of growing plants. This process is so widespread in arctic and subarctic lands that its effect upon vegetation is of primary significance. In thinking about the development of plant communities on such surfaces, we must become accustomed to thinking in terms of a relatively permanent physical instability of the soils.

It appears clear that the very bases upon which our concepts of dominance and primary biological succession have developed—the relative stability of surfaces—do not exist over wide areas in the boreal regions. It follows that vegetational dynamics in general for these regions must be developed upon a new conception of land form dynamics.

The study of arctic and subarctic land forms is still in its infancy though rapid progress is now being made. The United States Geological Survey, through its Alaska Terrain and Permafrost Section, has been concentrating on the problem during the past three or four years, and we are beginning to find some order in the chaos of newly observed facts. New aspects of the problem, however, are appearing constantly, and undescribed land forms due to frost are turning up each time a party goes into the field. There is beginning to appear, however, a concept of the molding of the landscape by frost action. It is called "cryoplanation," as opposed, perhaps, to peneplanation in temperate regions (Bryan, 1946).

Soils that owe their form and texture to frost action are now being called "congeliturbates," and the process that forms them is called "congeliturbation."

Some curious reversals of our commonly accepted ideas have developed. On a steep mountain slope, for instance, we are accustomed to thinking of small rocky stream channels and gullies as the most unstable plant habitats. In the Arctic, on the other hand, such stream channels, though they are very poorly represented, turn out to be the most stable habitats, for the presence of even a small running stream has a tendency to lower the water table slightly and so cut the supply of water to the surface soils immediately along its banks. The principal effect of this is to lessen the activity of frost, so that the materials along the banks of the stream actually stay in place for longer times than those on surfaces without streams.

Forests that develop on actively moving slopes are more or less unstable depending upon the degree of slope and drainage of the soils. The mortality in such

FIGURE 4. "Drunken forest" of black spruce growing on frost-heaved soil, in southwestern Yukon. Scarcely a tree is straight and vertical, and mortality is high.

forests is high, because when masses of soil move they have a tendency to tear the root systems of the trees loose from their intimate soil contacts. If the break is not too serious the trees can recover, but many of them do not. It is not uncommon to find 25% of the standing trees in a forest dead. Examination of growth rings shows that the trees have been subjected to this influence repeatedly. The evidence is in sudden suppressions of growth, with subsequent gradual adjustment. Usually no two trees show the same series of suppressions, even though they may be within ten feet of each other, because the soils move in finite masses which may be only a few feet in diameter. A characteristic of these forests is the large number of leaning trees which have been tipped over by the movement of the soils.

In the region as a whole, the only soils that are capable of developing a degree of mesophytism as we know it are those that are very well drained.

In many parts of the temperate regions where subaqueous erosion and deposit have been the rule we are accustomed to find hill slopes deeply gullied, with the surfaces modified by outcrops of bedrock that produce talus accumulations below and coves above. The deformational processes have produced extensive sorting of materials, both vertically and laterally, so that water tables are highly irregular in their relation to the surfaces. At the same time the rate of leaching and the development of soil profiles have been rendered highly variable from place to place. These are all variations in site, which are reflected in vegetational differences that appear in both vertical and horizontal arrangement.

One of the outstanding features of vegetation on slopes that are highly modified by cryoplanation processes is its lateral and vertical uniformity. Such variety as it possesses is so local and uniformly distributed that its effects are submerged in the mass. Examination of the soils on these slopes shows a very great uniformity in texture and in the position and behavior of the water table. Although the soils may be extremely unstable physically, the instability is so evenly distributed that an aspect of uniformity in the vegetation is maintained. The processes of cryoplanation, then, seem to have a strong tendency to form relatively smooth slopes upon which the sorting of fine and coarse materials is local and of small areal extent.

It is justifiable at this point to ask whether or not these findings in the study of boreal land forms and vegetation are of any immediate use to us who are concerned with problems at or near the glacial boundary. The effects of frost action are quite obviously a function of climate, and it is entirely justifiable for us to assume that climates in front of the advancing and disappearing glaciers were intensely cold. We are justified in looking, therefore, for the effects of this climate and its attendant frost action in the soils and topography in both the glaciated regions and beyond the glacial border. We probably must also insert in our sequence of events in the development of postglacial vegetation a period of time during which there must have been instability of soils and vegetation similar to that now occurring in the Arctic and Subarctic. The length of this period of time is as yet unknown.

Interpretation of our modern vegetation in terms of the periglacial climates should be approached circumspectly, and with full understanding that even in the Arctic where congeliturbation is still active and a major factor, its relation to vegetational dynamics is very imperfectly known.

I have suggested that it is necessary for us to insert in the sequence of postglacial vegetational changes a period of time during which the soils were unstable due to frost action. The cover of vegetation in this period had to be of plants capable of withstanding the instability. We have only small inklings of the floristic character of this vegetation. If we follow the classical interpretation of glacial and postglacial vegetational events we would assume that the plant cover was tundra and composed of arctic species. In this, however, we would be faced with our failure, to date, to find good evidence of an arctic tundra flora at the bases of our American peat profiles. We can get some suggestions, perhaps, by looking at the behavior of modern boreal floras with relation to stable and unstable soils.

The most important division in the boreal vegetation is that between forest and tundra, whether the latter be alpine or on the arctic plain. The timber line is generally regarded as a climatic phenomenon, and its fluctuations are thought to reflect climatic changes. In view of our growing knowledge of boreal soils it is possible to interpret the timber line as a zone of transition from relatively stable to relatively unstable soils, and to look upon the climate as having an indirect effect through its influence upon congeliturbation.

The white spruce, as a species, seems to cross the arctic isotherms at will. It can be found hundreds of miles north of the recognized timber line. Such northward projections, however, are on stream banks and narrow flood plains, or on sandy outwash plains where frost action in the soil in minimal or non-existent. The timber line itself might be thought of, then, as the zone in which the spruce can survive in numbers on the uplands due to the gradual southward amelioration of the extreme instability of the tundra soils. On the other side of the timber line, whether it be southward or at lower elevations on mountain slopes, the spruce fails to survive wherever congeliturbation is unusually intense.

For the majority of species in the boreal flora the timber lines are essentially impassable barriers. When a representative group from the whole flora is mapped, however, it is surprising how many species do cross this barrier with impunity. Of 283 species that I mapped some years ago (Raup, 1947), about 40% proved able to do it. Some of these are arctic species that range as far south as the Great Lakes and New England, while others are forest species that extend into the arctic islands. They must have extraordinarily broad tolerances in their relations to temperature, moisture, photoperiodism, and to instability in the soils. There must be, in any one species population, an abundance of genetic biotypes that gives the aspect of extreme plasticity to the species as a whole.

I believe it safe to say, therefore, that the present flora at nearly any point in boreal America has in it a group of species potentially capable of withstanding the rigors of intensified congeliturbation should the latter occur. Some of these species would be of arctic affinity, but many would be sub-boreal or even north temperate. A point chosen in the tundra west of Hudson Bay would show a high percentage of the former, while one taken in the heavily forested regions farther south would have a preponderance of the latter. Whenever we find soils in the Canadian forest that are actively stirred by frost this proves to be the case, and they are populated by species from the local flora.

I think it not impossible that we now have in the region of the glacial border species whose ranges of tolerance are or were sufficient to allow them to survive the periglacial climate with its attendant instability of soil. They can be looked for among those that are closely related to or identical with species now having wide ranges in the north; or they may have included southern species that had northern biotypes which have since been lost.

These facts and suppositions suggest that the region of the glacial border here in eastern America had no arctic tundra in the strict sense of the term during glacial and postglacial time. It probably had a few alpine plants derived from the pre-Wisconsin alpine floras of the New England mountains and the Adirondacks, and it probably looked like tundra physiognomically; but its predominant species might well have been derived from the native flora.

Dr. Denny in his contribution to this symposium will speak in considerable detail of the evidences of periglacial climates near the drift border. I shall mention only briefly some things that we have seen in central New England and other parts of the Northeast.

A view of the landscape in the neighborhood of the Harvard Forest at Petersham, Massachusetts, particularly if one can be found that is not covered with trees, shows the same broadly rounded slopes and hilltops that are now seen in the Arctic as a result of cryoplanation. These surfaces are characteristic of the upland tills of our region. Dr. Denny will show you the same kinds of surfaces in areas outside the glacial boundary.

When we examine these slopes in detail, we find that their microtopography is composed of broad terraces strongly reminiscent of those seen on arctic slopes (Stout, 1950). Some of them are banked on their fronts by masses of boulders such as one sees now on the alpine slopes of Mt. Washington and throughout the Arctic. The tills and small lenses of outwash within these terraces are found to be bent and involuted in such a way as to prove conclusively that the terraces have been formed by the slumping of masses of material down slope. Many of the terraces have slightly concave surfaces and are so strewn with boulders that they closely resemble the characteristic "block fields" of the arctic and alpine regions. Here and there are rock streams with many of their boulders still on edge, and occasionally one finds well-defined stone rings.

All of our tills in that part of New England are covered with a silt loam which varies considerably in texture and water-holding capacity due to the varying amounts of coarser materials that are incorporated in it. We now believe that the fine materials of this loam were deposited by wind and derived from glacial outwash plains in the vicinity. They have acquired their coarse materials, stones and boulders, by the same intense frost action that stirred the deeper tills. Evidence for this is to be found in the fact that the loams are worked into the terrace formations along with the underlying tills, and that they show evidence in themselves of the sorting of coarse and fine materials that is seen in arctic soils of similar nature.

It is of interest to carry this study into a still more specific problem (Stout, 1950). On some of our till slopes at the Harvard Forest we have been aware for a long time of peculiar discontinuities in the mixtures of red oak and white ash. There are concentrations of white ash interspersed with other concentrations in which red oak predominates. All of these are growing on lands that were in pasture before 1850. The lands have gone through the white pine stage characteristic of old fields in our area. The pines were logged off in the first and second decades of the present century, and the land is now taken over by hardwoods. We have always assumed that the variation in hardwood types was due in large

FIGURE 5. Ancient stone rings at the base of a slope near sea level in the lower Margaree Valley, Cape Breton Island, N. S.

part to chance. We have thought that the concentrations of white ash were due to the presence in the neighborhood of the old pine stands of old ash trees that supplied an abundance of seed, and that the oak concentrations had a similar explanation. The soils on these slopes have been mapped by the Bureau of Soils as essentially uniform.

We now find that the underlying tills on the slopes are composed of fine materials which are capable of holding up the water table for a considerable part of the growing season. We also find that the overlying loams differ widely in thickness, ranging from depths of 40″ to depths of 8″. Wherever the distance from the surface down to the fine textured tills is 20″ or less, we have concentrations of white ash. If the distance is more than 20″, we have concentrations of red oak. When we examine the distribution of the relative thickness of the loams, we find that it is closely correlated with the structure of the cryoplanation terraces. The loams tend to be thickest near the fronts of the terraces, and thin on their upper margins.

From these observations, we come to the tentative conclusion that the present local distribution of red oak and white ash in this area was determined by the reworking of glacial and wind-blown soils that occurred during the period of instability after the retreat of the last ice.

When we look at any large area of the slope, however, we note a remarkable uniformity in forest type and growth form. This uniformity is the rule rather than the exception in the hill country of New England and the Maritime Provinces. Where breaks occur in it they usually can be laid to human intervention or natural cataclysms. The natural types may change regionally from the central hardwoods of southern New England to the spruce and fir of the North; but within each type, differences that can be correlated with altitude or laterally arranged erosional features are uncommon. The principal variations that one sees are the extreme ones of the alpine zone in the White and Green Mountains, the flood plains of the larger streams such as the Connecticut River, the glacial outwash terraces in the larger valleys, the upland swamps and bogs, and the coastal marshes.

FIGURE 6. An ancient stone stripe and solifluction terrace in a pasture at Petersham, Mass.

I suggest that here again we have a reflection, persisting to modern times and evident in present forest type distribution, of the cryoplanation processes that were most active under the periglacial climate. These processes left the slopes essentially smooth, with soils remarkably uniform in texture, and with water tables that have no great variations in their levels beneath the surface.

Needless to say, a generalization such as this, if it should prove tenable, can have far-reaching repercussions in our future plans for the use of these lands. The silvicultural management of the forests, especially, will be conditioned by it.

I find myself concluding, from observations I have made and such reasoning as I have been able to accomplish with them, that the physiographic ecology of the temperate regions is inadequate for the rationalization of vegetational phenomena in the boreal regions. It appears necessary for us to derive a new kind of vegetational dynamics that will correlate with physiographic processes the chief agent in which is frost rather than running water. I conclude further that though these processes are now largely confined to boreal and alpine regions, they were formerly effective far southward, and at low elevations, even beyond the boundaries of the glacial ice. Their effects here upon soils and surfaces were so extensive that they still obtain and are strongly reflected in the nature and distribution of our natural vegetation.

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